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Age at puberty of channel catfish, *Ictalurus punctatus*, controlled by thermoperiod

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ABSTRACT

One of the major difficulties in selecting for superior traits for the culture of channel catfish is that most fish do not breed until they are three years old. This study was designed to decrease the time necessary to achieve puberty in channel catfish *Ictalurus punctatus*. Channel catfish, held under a shortened annual temperature cycle of four months of 26 C water followed by two months of 13–14 C temperature spawned at a higher rate (73%) after three temperature cycles than fish held in outdoor ponds on two normal seasonal temperature cycles (10%) or fish raised in tanks supplied with constant 26 °C water (3%). The fish were exposed to constant light in tanks until they were about 22 months old when they were stocked into outdoor spawning ponds with spawning containers. Fish held in constant warm water weighed about 1200 g and were significantly heavier than fish from the other two groups (about 600 g) when stocked into spawning ponds. Spawns from tank raised fish were significantly heavier than spawns from fish held in ponds and the shortened annual temperature cycled fish. These data suggest that the onset of the first reproductive period (puberty) is a developmental event that requires three cycles of warm and cold periods, and that weight and photoperiod have little influence on the onset of puberty.

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1. Introduction

One of the major difficulties in selecting for superior traits for the culture of channel catfish is their long generation time. Spawning success in two-year-old fish is very low and a high percentage of female fish usually spawn when they are three years old. The normal spring reproductive pattern in channel catfish is characterized by gonadal recrudescence that reaches a maximum in May with synchronous gonadal development and peak spawning in May and June. Females typically spawn once a year. Factors which determine sexual maturation in fish are not well understood, but such characteristics as age, size, and number of annual cycles are the most often mentioned features thought to influence puberty. These characteristics can be separated in fish by altering the temperature cycles under which they are raised. Since fish do not feed well at low temperatures, fish fed to satiation will grow differentially when part of the period is cold and they do not feed well. A number of fish species have been induced to spawn out-of-season by manipulation of temperature and photoperiod (MacQuarrie et al., 1979; Bromage et al., 1993; Devauchelle et al., 1987; Arnold, 1988; Kohler et al., 1994; Smith and Jenkins, 1988; Blythe et al., 1994). Kelly and Kohler (1996) were able to induce multiple annual spawns from mature channel catfish by manipulation of temperature and photoperiod, however, a short photoperiod was always used with low temperature and a long photoperiod was used with higher temperatures. Braughn (1971) achieved a spawning delay of several months of spawning by holding channel catfish at cool temperatures during the normal spawning season and then exposing them to spawning temperatures. In general, photoperiod appears to be the environmental factor inducing reproductive events in salmonids, flatfishes, temperate basses, sunfish and mullets (Bromage et al., 1993) and temperature induces reproduction in many cyprinids and other warmwater fishes (Horvath, 1986). Less information exists concerning the advancement of puberty, the first reproductive season. Early maturation of males is a well-known phenomenon in many salmonid species, and both genetic and environmental factors have been implicated in its occurrence (Naevdal, 1983; Thorpe et al., 1983; Rowe and Thorpe, 1990; Simpson, 1992; Silverstein and Hershberger, 1992; Crandall and Gall, 1993). Early maturation in females rarely occurs (Sutterlin and MacLean, 1984; Shimma and Kitamura, 1987). An early maturing strain of amago salmon (*Oncorhynchus masou ishikawae*) has been developed at the National Research Institute of Aquaculture in Japan. Feeding a restricted amount of feed to amago salmon resulted in a significant reduction in the rate of maturation in females (Silverstein and Shimma, 1994). Further, within the low feed group and the high feed group, the mature individuals were significantly larger than immature fish. The effect was less pronounced in males. A later study indicated that size or energy storage threshold must be surpassed for maturation to occur and that faster growing individuals matured at an earlier age (Silverstein et al., 1997). None of these studies compared size differences with age and the number of annual temperature cycles the fish were exposed to. The ovaries of two-year-old channel catfish have a seasonal pattern of development, however, the

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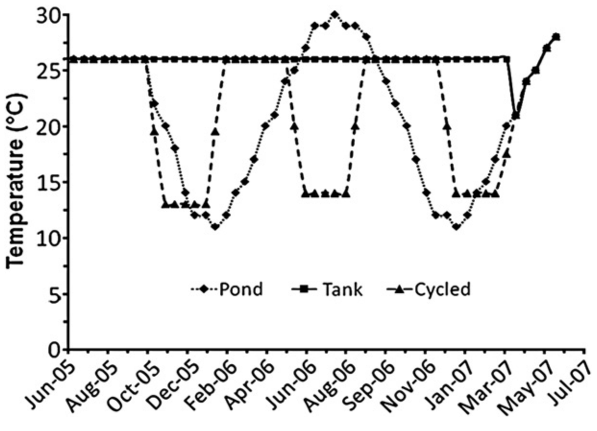

Fig. 1. Diagram of the experimental temperature conditions to which the three groups of fish were exposed.

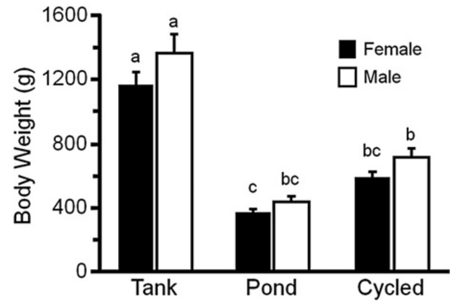

Fig. 2. Body weight (g) of 22-month-old channel catfish at the time of stocking into spawning ponds. Tank fish had been exposed to constant 26 °C water, pond fish were held in outside ponds under natural conditions, and cycled fish were exposed to alternating temperatures cycles of 2 months of 12–14 °C water followed by 4 months at 26 °C. The fish in the ponds had been exposed to 2 cold periods and the fish exposed to the shortened cycle had been exposed to three cold periods and three warm periods. Columns represent the mean + SE for 10 fish. Significantly different subsets by Tukey's multiple range test ($P<0.05$) are indicated by different letters.

magnitude of the GSI is about one third that of three-year-old fish, (Davis et al., 1986). Further, only about 10% of two-year-old fish spawn whereas about 60% of three-year-old fish spawn.

Channel catfish in ponds are exposed to annual temperatures that range from 35 °C in the summer to around 10 °C during the winter. The fish do not feed aggressively from about mid-October through mid-March (Dupree, 1984) and therefore most growth occurs during the warmer period. The present study was designed to determine if sexual maturation is dependent on fish size, fish age or the number of annual temperature cycles to which they are exposed.

2. Methods and materials

Experiments were conducted at the Catfish Genetics Research Unit USDA/ARS in Stoneville, MS located in west central Mississippi (33 26' 17.13″N, 90 53′ 48.30″W). Three spawns from different pairs of channel catfish which had undergone three generations of selection from the original NWAC 103 line, designated here as USDA 403 strain, were combined. Spawns were collected from spawning ponds in June of 2005. They were then raised together in the hatchery with flow-through well water at 26 °C. In mid-October of 2005 the fish weighed about 12 g and about 250 fish were randomly divided equally among three environments. One group was stocked into 150-l tanks with flow-through water at 26 °C, and was designated as tank (*T*), the second group was stocked into 0.04 ha ponds, and was designated as pond (*P*), the third group was held in tanks under a compressed annual thermal cycle of 4 months at 26 °C, and 2 months at 13–14 °C, and was designated as cycled (*C*). Lights were on in the tank room constantly for both the fish held in the tank environment at constant temperature and those in the annual compressed cycle. Fish in ponds were exposed to a natural photoperiod. Fish were fed to satiation daily with a 28% protein commercially available catfish feed. When fish in ponds or in thermocycled conditions were in temperatures less than 15 °C food was offered only once a week as suggested by Dupree 1984. The design of the experimental protocol is shown in Fig. 1.

In mid-April of 2007 all fish were 22 months of age. Fish from each group were stocked into 1.5 m deep 0.04 ha ponds. Pond temperature was about 20 °C, therefore fish were transferred to an outdoor concrete tank filled with 26 °C water and allowed to cool down to about 20 °C before being stocked in the spawning ponds. Prior to stocking, 10 fish from each thermal regime were sampled. Fish were euthanized with excess tricaine methanesulfonate, MS-222 (Argent Chemical Laboratories, Redmond, WA). Body and gonad weights were taken and a blood sample was taken with a heparinized syringe. The plasma was separated and stored at −80 °C for later analysis. The gonad weight was expressed as the GSI calculated as the % body weight.

Spawning techniques followed those recommended by Kelly (2004). Thirty female fish were stocked with 20 male fish and 10 spawning cans per 0.04 ha pond. At the time of stocking in the spawning ponds the cycled fish had been exposed to 3 warm temperature periods and 3 cold temperature periods. Fish held in the ponds had been exposed to 2 summer periods and 2 winter periods.

Female plasma samples were analyzed for testosterone and estradiol and male fish were analyzed only for testosterone by radioimmunoassay (Siemens Medical Solutions, Los Angeles, CA, Catalogue Nos. TKTT2 and TKE25, respectively). Concentrations are reported as ng/ml for testosterone and pg/ml for estradiol. The testosterone assay was validated by using a pooled sample of plasma from male channel catfish containing 1.2 ng/ml testosterone. Three replicate samples were determined to have 1.43 ng/ml, a 1:1 dilution was 0.7 ng/ml (0.6 expected) and a sample spiked with 8 ng/ml was determined to be 11.5 ng/ml (9.2 expected). The estradiol assay was validated using a pooled sample of plasma from female channel catfish containing 8 pg/ml. It was necessary to dilute the plasma

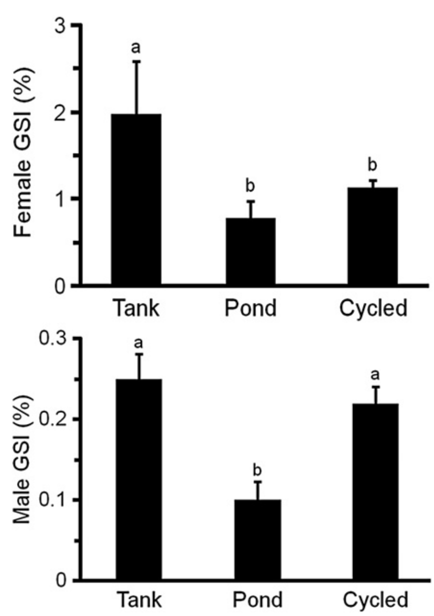

Fig. 3. Gonadal development (GSI) of 22-month-old female, upper panel, and male, lower panel, channel catfish at the time of stocking the fish in spawning ponds. The conditions that the fish were raised under are described in the legend for Fig. 2. Columns represent the mean + SE for 10 fish. Significantly different subsets by Tukey's multiple range test ($P<0.05$) are indicated by different letters.

sample by adding 100 µl of sample to 400 µl of water to read on the curve. Three replicate samples were determined to have 8.03 pg/ml, a 1:1 dilution was 2.8 pg/ml (4 pg/ml expected), and a sample spiked with 0.5 pg/ml was 9.5 (8.5 expected).

Differences among the groups were analyzed by analysis of variance followed by Tukey's multiple range test when significance ($P<0.05$) was indicated.

3. Results

When the fish were stocked in the spawning ponds in early April, fish raised in tanks were almost twice as heavy as those raised in the pond or those in the cycled environment. The weight of the cycled fish and fish held in ponds were similar. Male fish were generally heavier than females; however, males were not significantly heavier than females when stocked in the spawning ponds (Fig. 2.).

The GSI of the female fish raised in ponds was similar to that of the fish raised under the shortened annual temperature cycle and both groups were lower than fish raised in tanks (Fig. 3) at the time of stocking in the spawning ponds. However, plasma estrogen and testosterone were significantly higher in pond and tank raised fish than they were in the fish in the cycled environment (Fig. 4.).

The GSI of male fish raised in ponds was smaller than that of the fish raised in tanks or under the cycled regime. The GSI of the cycled fish was similar to those in tanks at the time fish were placed in spawning ponds (Fig. 4), however, there was no significant difference among the three groups in plasma testosterone concentrations (Fig. 4).

The first spawn was from the cycled group and was collected on May 24. By July 23, 73% of this group had spawned (Fig. 5.). The average weight of 16 spawns was 118.6 + 11.1 g (mean + SE). On August 1, 2007 the only spawn (3%) from the tank raised fish occurred. This spawn was very small and was likely a partial spawn. The spawns from the cycled fish were significantly heavier than the three spawns (10%) collected from the pond raised fish, on June 28, July 6, and July 19 which averaged 48.3 + 19.0 g.

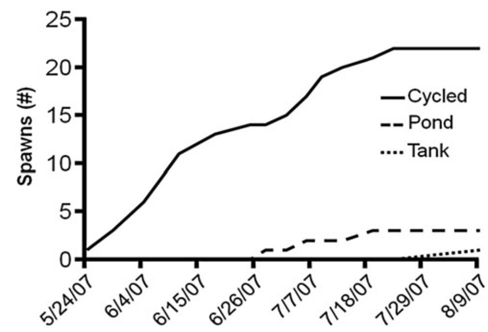

Fig. 5. Cumulative spawning success of the fish raised under the conditions described in the legend for Fig. 2. Thirty female and twenty male fish from each treatment were stocked into each pond with 10 spawning containers.

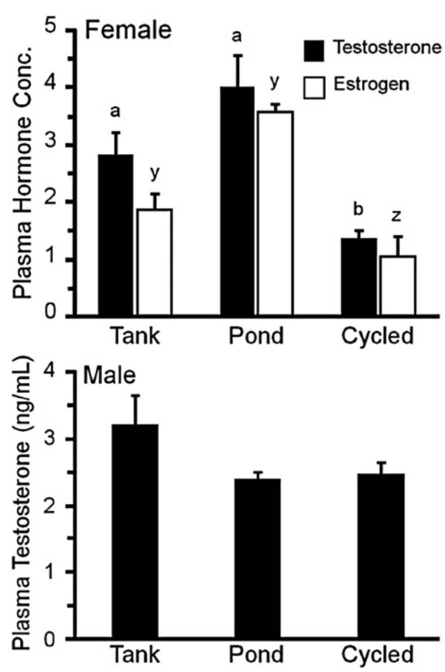

Fig. 4. Plasma testosterone (ng/ml) and estradiol (pg/ml) concentrations of 22-month-old female, upper panel, and plasma testosterone in male, lower panel, channel catfish at the time of stocking the fish in spawning ponds. The conditions that the fish were raised under are described in the legend for Fig. 2. Columns represent the mean + SE for 10 fish. Significantly different subsets by Tukey's multiple range test ($P<0.05$) are indicated by different letters.

4. Discussion

The data presented here suggest that body weight and age of the fish are relatively unimportant in attaining sexual maturation and that puberty is a developmental process dependent on the number of annual temperature cycles to which the fish are exposed. At least three periods of cold temperatures appear to be essential in developing full sexual maturity. This is further supported by the spawn weights of the cycled fish which were significantly heavier than the pond raised fish while the body weights of the fish were similar. The photoperiod also seems to play no role in the development of puberty of channel catfish. Catfish which were bilaterally enucleated or pinealectomized could still detect the timing of the light cycles where fish both bilaterally enucleated and pinealectomized could not (Goudie et al., 1983). Bilaterally enucleated and pinealectomized two-and three-year-old fish had annual cycles of female gonadal development similar to normal controls. Three-year-old fish had gonadosomatic indices and plasma estrogen concentrations about twice that of two-year-old fish. Further, spawning success (%) and timing of spawning was similar among control, enucleated, pinealectomized and enucleated and pinealectomized channel catfish (Davis et al., 1986). Surprisingly, neither the GSI nor plasma sex hormone concentrations provided any predictive value as to which treatment would result in the highest spawning success at the time of stocking in the spawning ponds. Treatment with sex hormones has been found to advance gonadal differentiation and spermiation in sea bass *Dicentrachus L* (Zanuy et al., 1999) and black carp *Mylopharayngodon piceus* (Gur et al., 1995), and grey mullet *Mugil cephalus* (Chang et al., 1999). Feed restriction which resulted in fish which weighed half that of the fish without feed restriction reduced early maturation of female amago salmon *Oncorhynchus masou ishikawae* by 32% but males were unaffected (Silverstein and Shimma, 1994). Additional studies on amago and Chinook salmon *Oncorhynchus tsawtscha* have suggested that larger size had the primary effect on earlier puberty but that increased fat content in smaller fish also played a role in early maturation (Silverstein et al., 1998). These experiments led to the proposal that a size or an energy threshold must be surpassed for maturation to occur (Silverstein et al., 1997). In the present study only one spawn was collected for the fish raised at the constant high temperature. These fish were fed daily and were about twice the weight of both the pond raised fish and the fish exposed to the thermal cycle. Although there are previous papers describing out-of-season spawning in channel catfish this work is the first to describe the early induction of puberty and to show that fish size alone is relatively unimportant. The present data suggest that annual thermal cycles are more important to the induction of puberty than size. By shortening the periods of alternating warm and cold temperatures it may be possible to decrease the time to puberty to one year. The fish and therefore the resulting spawns would be expected to be smaller than those produced by larger fish, however, if the selection of desirable traits from subsequent generations was more important that fish numbers, selection of those traits could be increased dramatically.

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